VOL. XV, No. 6 NOVEMBER-DECEMBER, 1954

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BORDEN'S REVIEW

of

NUTRITION RESEARCH

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PHOTOSYNTHESIS

BORDEN'S REVIEW
of
NUTRITION RESEARCH

Reviews and summaries of research information concerning nutrition and foods. Published bi-monthly, by THE BORDEN COMPANY; officers of the Company: Theodore G. Montague, president; E. L. Noetzel, treasurer; D. T. Orton, secretary. Editorial office: 350 Madison Avenue, New York 17, N. Y.

PHOTOSYNTHESIS

By FARRINGTON DANIELS, Ph.D.*

Food for men and animals, heat for houses and fuel for engines — all came originally from the energy of the sun through photosynthesis. Of all the ingenious ways by which a modern scientist might seek to utilize the sun's energy and store it, none has approached in effectiveness the ordinary growth of plants — a process which, in the presence of sunlight and chlorophyll, combines carbon dioxide from the air, with water and traces of inorganic salts from the soil to give carbohydrates and other organic material. Nature carries out many remarkable chemical and biological reactions, but none are more challenging than photosynthesis. It apparently goes the wrong way! Carbohydrates will burn spontaneously in oxygen with the evolution of large amounts of heat, and if the reaction is made to proceed in the opposite direction, large amounts of energy must be introduced. A theoretical scientist living in isolation would probably predict that this reaction could not be reversed with the energy of sunshine; first, because carbon dioxide and water do not absorb the sun's radiation; and second, because the units of radiation have only about one-third as much energy in them as the minimum energy required for a molecule of carbon dioxide to react with a molecule of water, and there is no way by which several units of radiation can be made to collide simultaneously with two molecules to supply the necessary energy of reaction.

And yet photosynthesis has been going on for many hundreds of millions of years. Growing crops supply many of our needs, but our requirements for energy to run our mechanized age are so great that we cannot begin to meet them, year by year, with agricultural crops. We have to draw on the photosynthesis of the past. Occasionally some of the products of photosynthesis have been buried by geological accidents and preserved as coal, oil and gas for our use. At the present time in the United States we are putting fifty times as much energy into our machines in the form of fuel as we are putting into our people as food. The mechanization of the world is rapidly increasing.

How long will we have fuel? What will we do when we have used up all our fuel reserves? We will develop atomic energy and new ways of using solar energy directly. Photochemical substitutes for photosynthesis are theoretically possible and more promising in the long range view than the use of solar energy in heat engines, but there is no mechanism yet in sight whereby

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energy can be stored chemically without the living cell. The fact that this photosynthesis actually does occur in nature is a challenge, however, to scientists to find new chemical ways of storing the energy of the sun. We are just beginning to understand fully the mechanism of this remarkable process.

Facts of Photosynthesis

The chemical reaction is written $CO_2 + H_2O + \text{light} \rightarrow (CH_2O) + O_2$ where the (CH_2O) represents a carbohydrate corresponding to one gram atom of carbon. Many of these units combine to give sugars, or cellulose.

There are many interesting facts which will eventually be pieced together to explain the process of photosynthesis, and more are being discovered rapidly.

One of the early quantitative experiments by Blackman showed that the rate of photosynthesis is directly proportional to the intensity of light up to a certain limit and then the rate is the same no matter how much the light is increased. The relation is shown diagrammatically in Fig. 1.

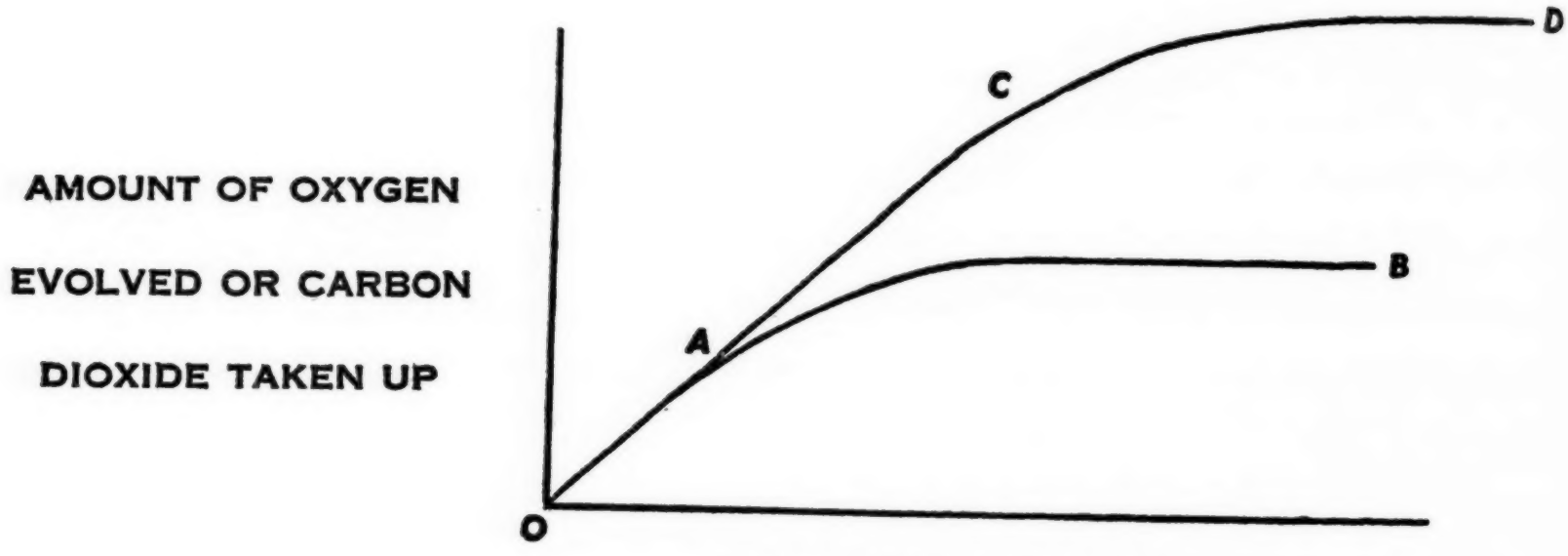

Fig. 1 — Relation Between Light Intensity and Rate of Photosynthesis

The region of direct proportionality OA is known as the Blackman region and for algae and most plants, it extends from the limits of very low light intensity up to about 10 Kergs per second per sq. cm. The intensity of bright sunlight is of the order of 800 Kergs per second per sq. cm. or 1 calorie per sq. cm. per minute, so that in much of agriculture the light is too bright to be fully utilized.

The explanation of Blackman's phenomenon is obvious. In photosynthesis the first step is a photochemical reaction which is followed by other reactions taking place in the dark to give the final products. At low light intensities the photochemical step limits the rate of the overall process, but

at high light intensities one of the dark reactions becomes limiting. The photochemical reaction supplies "food" for the plant to digest and at low light intensities the plant digests it as fast as it is provided. But if the food is brought in too fast, the plant cannot use it immediately and the rate of digestion becomes the limiting rate. Moreover, the accumulated products of the photochemical step may be photo-oxidized, under some conditions, back to carbon dioxide and water. Although the intensity of sunlight is greater in the tropics than in the northern latitudes, the longer days of the northern areas and the greater efficiency at the lower light intensities may give a more effective photosynthetic yield.

Any change which increases the rate of the dark reaction will increase the rate at which the first photosynthetic product can be assimilated and thus increase the yield when the light intensity is limiting. It raises the level at which proportionality between light and photosynthesis is maintained.

Since most chemical reactions at room temperature double or treble for a 10°C. rise in temperature, the dark, thermal reactions of the assimilation process are accelerated by a rise in temperature and the Blackman region of direct proportionality extended to higher light intensities from OA to OC in Fig. 1. The temperature coefficient of the rate of photosynthesis provides a convenient way of studying the relative importance of the dark and light reactions, but the range of temperatures is limited from 0° to about 40° C. for most plant organisms.

The Blackman region can be extended to higher light intensities also by increasing the carbon dioxide concentration. It is only 0.03 per cent in air and in bright light the photochemical step cannot continue at full speed because the supply of carbon dioxide is not enough. Accordingly, in order to obtain maximum photosynthetic efficiency and growth in plants, it is customary in experimental work to increase the concentration of carbon dioxide to 3% or more.

Another important property of plant growth is the respiration which always accompanies photosynthesis. The plants take up oxygen and give off carbon dioxide just as animals do. When experiments are carried out in the dark, respiration is measured separately from photosynthesis and it is assumed that the same respiration is maintained during photosynthesis in the light. This seems to be a safe assumption, provided the periods of measurement in dark and light are sufficiently short to assure that the conditions have not changed between successive exposures to light. It is a necessary assumption in calculating the energy efficiency of photosynthesis.

Chlorophyll is the active material of plants for photosynthesis. It is a complex molecule somewhat similar in structure to hæmoglobin of the blood, except that it contains magnesium instead of iron. Its absorption spectrum

contains strong bands in the red and in the blue so that it has a marked green color. In thick layers, however, even the green light is absorbed and the light of all wave lengths in the visible region is equally effective in photosynthesis. Because the green light is the most intense in sunlight it is responsible for more plant growth in the world than light of any other color. There are other pigments in plants in addition to chlorophyll which absorb light. Usually they do not take part in photosynthesis, but in some cases they are effective, probably in conjunction with the chlorophyll which is also present.

The simple chemical reaction for photosynthesis, already given, consumes one molecule of carbon dioxide and produces one molecule of oxygen and one unit of a carbohydrate. The ratio carbon dioxide/oxygen is known as the respiration quotient and it should have a value of 1 if the reaction produces only carbohydrate. In fact, a large departure from unity suggests that there may be an error in the measurements of one of the gases. However, there are fats and proteins and many other chemical compounds in the plant products as well as carbohydrates but the ratio of carbon dioxide to oxygen is always near unity. Proteins require nitrogen which must be taken up in the form of nitrates from the water in which the plants grow. Calcium, magnesium, potassium and many other elements, such as boron, cobalt, zinc, tungsten and others, must be present also as nutrients to insure healthy growth. Each element takes part in some necessary intermediate chemical or enzymatic step. Most soils contain an adequate supply of these trace elements, but if there is a deficiency it must be corrected. Satisfactory synthetic nutrient solutions often contain twenty-five or more chemical elements added directly or present as impurities in the nutrient salts.

In single celled organisms like algæ, all parts take part in photosynthesis, but in higher plants there is specialization and only the leaves carry on photosynthesis, while the roots and stems of plants or the trunks of trees carry the chemical nutrients to the leaves and transport the carbohydrates and other photosynthetic products from them. Other parts of the plant store the chemical products for later use. Only the light which falls on chlorophyll-containing leaves can be used in photosynthesis. The chlorophyll is contained in small parts of the leaves known as chloroplasts and in these units it is further concentrated in still smaller units known as granna. In these granna there are layers of chlorophyll molecules held together with protein molecules like butter in a sandwich. In this way, the chlorophyll molecules are spread over an enormous surface and are thus available for the rapid exchange of gases. Even in the interior of leaves the carbon dioxide can diffuse in and the oxygen can diffuse out with great rapidity.

Energy Efficiency

When cellulose or a sugar is burned to give carbon dioxide and water (the reverse of the photosynthetic reaction), heat is evolved amounting to 112,000 calories for each gram atom (12 grams) of carbon oxidized. When a chemical reaction is reversed at least the same amount of heat must be absorbed as was evolved originally and so the carbon dioxide and water must absorb at least 112,000 calories in order to react. In fact, this is a minimum value because most reactions require an activation energy for reaction which is greater than the endothermic heat of the reaction. This large amount of energy must be supplied by the sunlight.

Furthermore, the dark thermal reactions involve heat and their energy, too, must be supplied from photosynthesis.

The exact amount of energy stored in plant growth can be measured by burning the dried plants in a combustion calorimeter. The ratio of the calories of heat evolved to the calories of sunlight absorbed by the plant during its growth gives the fraction of solar radiation permanently stored. Experiments of this type are interesting for overall efficiencies, and for comparison with agricultural crop efficiencies, but for absolute measurements of the photosynthetic efficiency, exposures of much shorter duration are necessary, so short that the conditions of respiration and growth are the same over the periods of light and dark. Ten-minute periods are frequently used and the increase in weight of the plant material is too small to measure. Very sensitive analytical methods are required to measure the rate of photosynthesis and respiration over these small time intervals.

In order to establish a quantitative relation, it is necessary to measure not only the amounts of carbon dioxide and oxygen, but also the quantity of energy introduced into the reaction by the light. In quantitative photochemical studies it is necessary to use monochromatic light, because each different wave length has a different amount of energy associated with it. The monochromatic light, produced by a prism or optical filters, is of low intensity, and special apparatus of high sensitivity is necessary to measure the chemical changes. The intensity of the light beam before and after passing through the algal cells is determined with a thermopile calibrated in absolute units, using a carbon filament lamp, standardized at the U. S. Bureau of Standards. This difference together with the time of exposure to the light gives a measure of the calories of light absorbed in photosynthesis.

It will be shown presently that 8 photons are required under optimum conditions to cause the combination of one molecule of carbon dioxide and one of water in photosynthesis. In red light which contains about 40,000 calories of energy in a mole of photons (6.02×10^{23} photons) the 8 photons

are equivalent to 8 x 40,000 or 320,000 calories per mole and they store up energy of 112,000 calories which can be released on burning the photo-synthetic product. The energy efficiency of photosynthesis, then, is about 112,000/-320,000 or 35 per cent. In blue light, the energy efficiency is about 20 per cent. The photon-to-molecule ratio is about the same as in red light and the energy per photon is about 70,000 calories per mole.

Many different methods of measuring photosynthesis have been used, mostly with algæ. The amount of light absorbed can be measured accurately in a glass cell filled with algæ, and the algal cells are thermostated by the surrounding water. The sunlight does not cause an increase in temperature at the surface as it does in the case of leaves of a land plant. The manometric method, as developed by Warburg, has been widely used for quantitative measurements. It depends on the fact that carbon dioxide is more soluble in water than oxygen and so a change in the total pressure of the gases in equilibrium with the algæ gives a measure of the exchange between carbon dioxide and oxygen both in photosynthesis and in respiration. Two requirements must be met — carbon dioxide and oxygen must be the only gases which change their partial pressures during the experiment, and they must be in complete and rapid equilibrium with the solution and with the algal cells in suspension. The situation is much more complicated with photosynthesizing algæ than with respiring yeast or bacteria because the change from dark to light and light to dark introduces a change within the algal cells of the rate and even the direction of the gas exchange. Any lag in this exchange may introduce serious errors in the interpretation of the pressure readings. A critical evaluation of the manometric technique for measurements of photosynthesis has been given by Emerson (1).

Warburg and Negelein (2) in 1923 were the first to make quantitative photochemical studies of photosynthesis. Using chlorella with red light and measuring the rate of photosynthesis with a Warburg manometer, they reported that 4 photons per molecule would produce photosynthesis corresponding to an energy efficiency of 70 per cent. These measurements were carefully made and were not checked for many years. From 1934 to 1954 a series of measurements on the energy requirements of photosynthesis have been carried out at the University of Wisconsin using several different methods of measurements including: microgas-analysis, chemical titration and electrical analysis for dissolved oxygen with the dropping mercury electrode. All the researches have given efficiencies of about 8 photons per molecule or lower efficiencies. In Fig. 2 are shown results by Moore and Duggar (3) with the dropping mercury electrode in which the ordinates give the concentration of dissolved oxygen in terms of galvanometer readings. Respiration and consumption of oxygen is going on continuously but when the

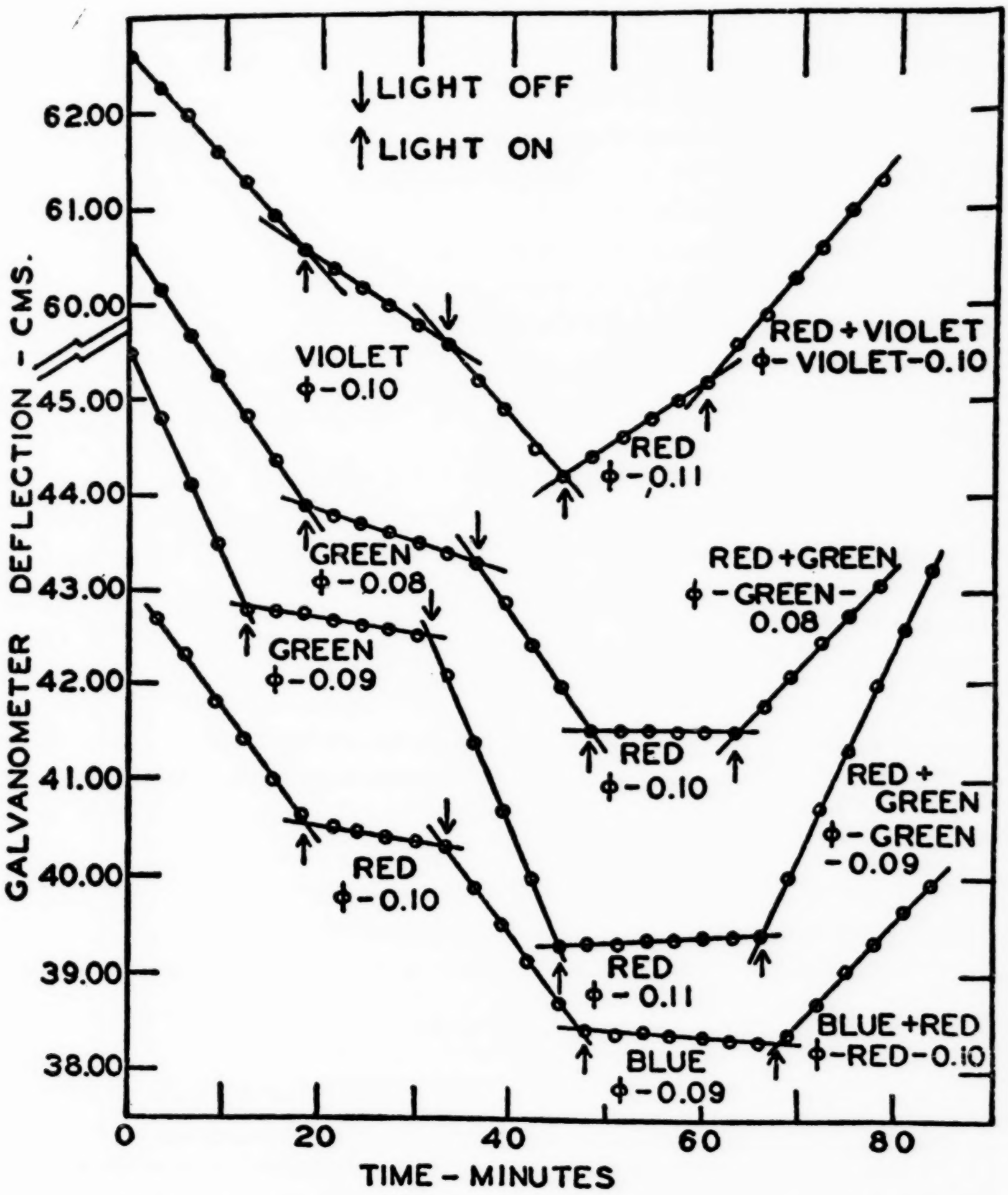

Fig. 2 — Changes in the concentration of dissolved oxygen with time in algal cell suspensions in light and in darkness, and the quantum efficiencies obtained.

algæ are exposed to light, oxygen is also evolved from the photosynthesis. If the light intensity is low the photosynthesis merely lessens the over-all rate of decrease in oxygen; if it is high the slope of the line is actually reversed and the oxygen evolution exceeds the absorption. When the light intensity is such as to make the photosynthesis exactly equal to the respiration, there is no change in oxygen concentration and the photosynthesis is said to be at the compensation point. In Fig. 2 the quantum yield (the num-

ber of molecules of oxygen evolved per photon) is indicated for each experiment. In these calculations the rate of oxygen change in the dark is subtracted from the rate in the light, and the energy absorbed is determined in absolute units. It is seen in Fig. 2 that most of the measurements of photosynthesis give about 0.1 molecule per photon or 10 photons per molecule and the results are nearly the same with different wave lengths of light.

In other experiments the algæ were placed in a microcalorimeter and the slight temperature rise was measured when a light beam was introduced. Eighty per cent as much heat was produced when the light was passed into algæ as when it was passed into a black solution of India ink, showing that not more than twenty per cent of the light energy was stored as chemical energy.

In the most recent experiments, the gases circulated through the algal suspension are analyzed for oxygen by magnetic moment and the carbon dioxide by infrared absorption (4). Here the concentration of each gas is measured specifically and recorded simultaneously. The respiration quotient was always close to unity and the average of some sixty measurements ranging from 7 to 11 photons per molecule was 8.9. A typical measurement is shown in Fig. 3.

These results of 8 to 10 photons per molecule obtained by several different methods have been checked by Emerson and his associates (5) and others, but Warburg, Burk and their associates continue to report 4 photons per molecule. The discrepancy cannot be due to differences in energy measurements because they have been cross-checked with actinometers; and it cannot be due to different algæ because all have been of the same type, and the results giving 8 photons per molecule have been consistent with algæ of many stages of growth over a period of several years. Emerson attributes the 4-photon results to a burst of carbon dioxide released by the first exposure to light after pretreatment in the dark, leading to a misinterpretation of the manometer readings.

No absolute theoretical limit to the energy efficiency is known except that it cannot be more than 100 per cent which corresponds to about 3 photons per molecule. Many biological processes such as the work done by animals seem to be less than 20 per cent efficient.

The difference between a laboratory maximum of 35 per cent and 70 per cent is of no significance in agriculture because the efficiency of the yield is so much smaller than these values. A good average farm crop produces one or two tons of dry organic matter per acre per year, which, on burning, will give back about 0.1 per cent of the annual solar energy falling on the acre of land. Hybrid corn on well fertilized land gives more; and sugar cane, growing the year around, can give considerably more. Forest crops, scienti-

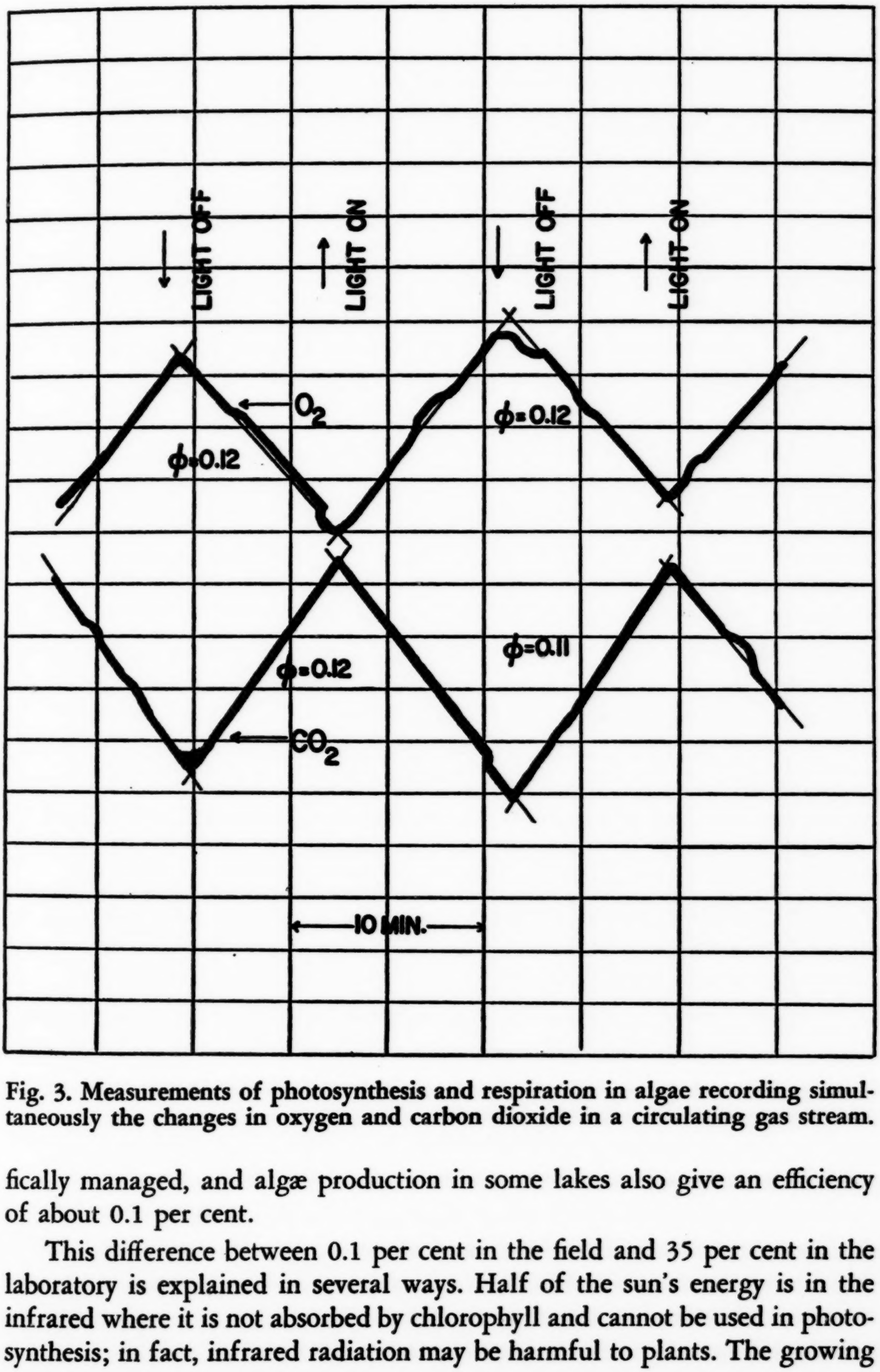

Fig. 3. Measurements of photosynthesis and respiration in algae recording simultaneously the changes in oxygen and carbon dioxide in a circulating gas stream.

fically managed, and algæ production in some lakes also give an efficiency of about 0.1 per cent.

This difference between 0.1 per cent in the field and 35 per cent in the laboratory is explained in several ways. Half of the sun's energy is in the infrared where it is not absorbed by chlorophyll and cannot be used in photosynthesis; in fact, infrared radiation may be harmful to plants. The growing

season is only about one-third of the year and the carbon dioxide content of the air is only about 0.03 per cent whereas in the laboratory experiments of high yield, it is kept at about 3.0 per cent. Moreover, the sunlight in the field is much too bright to give optimum photosynthetic efficiency; it is well above the intensity which governs the Blackman region of Fig. 1.

Agriculture does a reasonably good job of storing the sun's energy for later use, and its productivity will improve with further research, but in order to obtain very large increases in photosynthetic efficiency, it will be necessary to use radically different methods. Mass culture of algæ gives some promise of an increase of perhaps tenfold in productivity. Experiments at Stanford, California and at the A. D. Little Co. in Boston were carried out with long tubes of plastic filled with algæ in an atmosphere high in carbon dioxide. High yields were indicated, but there were difficulties with contamination by non-photosynthesizing organisms, and with overheating. Further research is needed to develop algæ which will photosynthesize efficiently in bright light and which will grow healthily in water at high temperatures. Although the yields of organic material are high in the mass culture of algæ, the capital investment, of course, is very high. The plastic containing-vessels, the circulating pumps, the carbon dioxide and the means for harvesting the algæ are expensive. If this method should come into demand for producing large tonnages of food the supply of carbon dioxide gas might become a limiting factor.

Fertilizer material, potassium, phosphate and nitrogen have to be supplied along with many other trace elements. Certain blue-green algæ can be grown without the addition of nitrates because they have some ability to fix the nitrogen of the atmosphere.

Dr. Tamiya in Tokyo has carried on interesting work on the mass culture of algæ using a stringy type of algæ which is easy to filter. His conditions of growth seem to produce less contamination. Furthermore, he has made several palatable foods from these algæ.

It is interesting to realize that carbohydrates and other direct plant products provide the most efficient food in transferring the energy of the sun directly into energy for men. If the plants are fed to animals and the animals used for meat, there is a considerable loss of original energy because the meat producing animals have to live their own lives and consume energy. The meat foods contain perhaps 10 to 15 per cent of the energy content of the original vegetable foods which they have consumed. This is the reason that populations which are living at a barely subsistence level with limited agricultural land and small sunshine area per person must have a vegetarian's diet. They cannot afford a meat diet with its less efficient conversion of solar energy.

Mechanism of Photosynthesis

The combination of a molecule of carbon dioxide with a molecule of water requires more energy than can be supplied by one photon of sunlight. The reaction evidently takes place in steps. It is quite well established now that when a photon of light is absorbed by a chlorophyll molecule the energy is transferred to a water molecule in such a way that a hydrogen atom is broken off. The hydrogen atom then reacts with carbon dioxide. A second photon acting on chlorophyll and water liberates another hydrogen atom which still further reduces the partially reduced carbon dioxide. This process continues stepwise until a carbohydrate having the general form (CH_2O) is formed. According to this mechanism, it is possible to bring about the overall reaction of more than 112 kilocalories, using photons of much lesser energy.

The experimentally determined energy efficiencies can be used to check certain mechanisms. For example, a mechanism which required the consumption of half of the absorbed sunlight would be ruled out because only about one-third of the energy is available.

Details of these chemical steps are being worked out. Franck (6) has studied these mechanisms in great detail and evaluated them critically. According to one set of reactions, there should be a requirement of 8 photons per molecule, close to the observed maximum efficiency. The respiration reactions which go on both in the dark and in the light are intimately connected with the photosynthetic reactions and probably several enzyme-catalyzed reactions are involved.

Qualitative attempts have been made to distinguish between the different enzymatic reactions by adding poisons. For example, when potassium cyanide or sodium azide are added in concentrations of about 1 x 10-4 and 1 x 10-5 moles per liter respectively, the photosynthesis rate is greatly reduced, but the respiration rate is hardly affected. These poisons are known to give specific inhibiting effects on certain enzymatic reactions which can thus be tentatively identified in the photosynthetic process.

Isotopic tracers provide another and very powerful method for learning more about the mechanism of photosynthesis. Radioactive carbon, C^{14}, in the form of carbon dioxide is taken up by the algæ during photosynthesis and the first products formed and successive products can be identified by their radioactivity. Calvin has done outstanding work in this field. Algæ are quickly killed, then they are placed in solvents which extract some of the organic compounds. These compounds are then identified by paper chromatography. A large sheet of filter paper is held in a slanting position and some of the solution is allowed to flow gently down at one corner. The

different organic compounds are adsorbed at different distances along the paper. The filter paper is then tilted at right angles and a second solvent is allowed to flow down the paper at right angles to the first flow. Again the several compounds are adsorbed at different distances along the paper. The filter paper is then placed for a few hours on top of a photographic film and wherever there is a chemical compound containing radioactive carbon a black spot will be produced on the developed film. The position of the exposed spot is measured along the X and Y axis and then a pure chemical compound containing radioactive carbon is found which produces radioactivity at the same spot under the same conditions of treatment and fractional adsorption on the paper. The position on the paper of each plant ingredient thus permits identification of the compound which may be an acid or sugar or any one of a variety of intermediate compounds. The experiments are repeated at several different time intervals following the introduction of the radioactive carbon dioxide. In this way it is possible to determine the first product of photosynthesis and the successive products in order. Calvin (7) has found that some of these products appear in the first few seconds after the radioactive carbon dioxide is introduced and others take a longer time for formation. He has proposed detailed mechanisms based on these findings.

Earlier work indicated that carbon dioxide is incorporated into carbohydrate molecules by a carboxylation reaction leading to the three-carbon compound phosphoglyceric acid. This acid is then converted into six-carbon compounds by a series of reactions. A search for a two-carbon compound, acting as an acceptor, was fruitless, but this type of a compound now appears to be unnecessary.

It has been found recently that the seven-carbon carbohydrate, sedoheptulose monophosphate, and the five carbon carbohydrate, ribulose phosphate, appeared with labelled radioactive carbon shortly after exposure to the radioactive carbon dioxide. There is a difference of two carbon atoms between these compounds and there is also a difference of two carbon atoms between ribulose and several three-carbon compounds.

The photosynthetic cycle now proposed by Calvin involves carboxylation of ribulose to two molecules of three-carbon compounds, probably phosphoglyceric acid. In the cycle, both sedoheptulose and ribulose diphosphate are formed from tricose and hexose phosphates. Hexose in turn is synthesized by reducing 3-phosphoglyceric acid. Free energy calculations show that the ribulose carboxylation reaction is possible spontaneously if it is enzymatically catalyzed.

Although many attempts have been made to bring about photosynthesis in the laboratory without the living cell no successful experiment has yet

been fully established. There seems to be no reason why photosynthesis in vitro is theoretically impossible and the search for new approaches will undoubtedly continue. A step toward this goal has been made in the Hill reaction which consists of chloroplasts from dead algal cells in an oxidizing solution of ferric chloride or quinone. When the chlorophyll is illuminated chemical reduction takes place. These materials are easier to reduce than carbon dioxide and the energy requirements are smaller, but nevertheless the first steps in photosynthesis appear to be produced in vitro. Hydrogen atoms liberated from water by photo-activated chlorophyll bring about reduction of an oxidizing agent. Even if a substitute for chlorophyll should be found, it probably could not be as plentiful and inexpensive as chlorophyll.

Conclusions

The facts of photosynthesis and the efficiency of photosynthesis as measured in the laboratory together with new experiments with isotopic tracers, provide a foundation on which to build a mechanism for photosynthesis. We are just beginning to understand this remarkable reaction which produces carbohydrates from carbon dioxide and water. Apparently, the sunlight activates chlorophyll which supplies sufficient energy to cause water to dissociate into hydrogen atoms which reduce carbon dioxide in successive steps to carbohydrates. The existence of photosynthesis acts as an encouragement and a challenge to find new and possibly better ways for storing and using the sun's energy directly.

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BRNR Reader-Survey Results

The advisory board of *Borden's Review of Nutrition Research* wants to thank readers for their generous response to our recent readers' survey. To date, over one-third of the individual readers have mailed their questionnaires—an overwhelming response, according to experienced survey-makers whom we consulted.

Here are some of the facts we learned through tabulations of 3,000 answers—a more-than-adequate count on which to project figures, say our statisticians.

> Nearly 60% of you read *all* articles in *Borden's Review.* More than 74% rate the *Review* "excellent" in informativeness and interest. 81% rate it "excellent" or "good" in terms of usefullness in your work. And 87% find it "excellent" or "good" as a source of literature references.

About half of the responses show preference for articles on basic research, while the remainder were divided in their preference for applied and clinical research.

Over 80% of you think the length of articles in *Borden's Review* "just right." Those who think some papers "too long" or "too brief" were just about evenly divided—6% and 5%.

The survey reveals these percentages of readers among the major professional or occupational groups:

Teachers (nutrition and related subjects)	21%
Nutritionists	20%
Physicians	13%
Dietitians	10%

Other groups represented include biochemists, laboratory directors, research people in commercial enterprises, dentists, home economists, students, writers, librarians and many others in highly specialized occupations.

Among the requests and suggestions for topics for future issues of *Borden's Review,* the greatest number were for specific phases of vitamin and mineral research. Next most-wanted topics concerned nutrition in treatment of major diseases. Proteins and amino acids were high on the request list, as were nutritional phases of geriatrics and pediatrics. Pregnancy and obesity were also among the frequently-requested topics.